

A SYSTEMATIC STUDY OF THE GENUS *BAHIA* (COMPOSITAE)¹

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Bahia, a genus in the tribe Helenieae, is restricted to North and South America, a single species only occurring on the latter continent. Increased attention has been given to the Helenieae within recent years by American workers,² due at least in part to geographic considerations and the fact that ample material, including many types, is available in herbaria in the United States.

Small (1919, p. 312) and Cronquist (1955), among others, have questioned the naturalness of the tribe Helenieae. Whereas no attempt is made in the present study to evaluate the taxonomic status of the tribe, the study of *Bahia* should eventually prove helpful in answering questions on this level.

The major phase of the study has been an assessment of the taxa which fall within the generic limits of *Bahia*. The judgments have been based upon field work in the area of major concentration of the genus, examination of some 2000 herbarium specimens, and garden and greenhouse cultures, as well as upon data derived from chromosome counts, biochemical (chromatographic) study and fertility tests. After consideration of the above data, the writer has recognized 15 taxa as belonging to the genus *Bahia*: 13 species (including one new one) and 2 varieties. It is believed that the present treatment clarifies the relationships of *Bahia* with

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²The following taxa have been monographed, revised or partially treated since 1950: *Baeria* (Ornduff, unpubl.); *Eriophyllum* and related genera (Carlquist, 1956); *Florestina* (Turner, 1963); *Gaillardia* (Stoutamire, 1958); *Helenium* (Rock, 1957); *Hymenopappus* (Turner, 1956); *Hymenothrix* (Turner, 1962); *Hymenoxys* (Parker, unpubl.); *Lasthenia* (Ornduff, unpubl.); *Palafoxia* (Turner, unpubl.); *Perityle* (Shinners, 1959).

other comparable groups in the subtribe Bahianae and places the species in natural genera which, it is hoped, are monophyletic.

TAXONOMIC HISTORY

The genus *Bahia* was named by Mariano Lagasca in 1816 in honor of Juan Francisco Bahi, professor of botany at Barcelona, Spain. It was typified by *B. ambrosioides*, a species described from a specimen presumably collected in the vicinity of Concepción, Chile, South America, by an individual now unknown. Nuttall (1818) described the first species of the genus recognized in North America, *B. oppositifolia*, as one member of his newly proposed *Trichophyllum*. De Candolle (1836), however, included *Trichophyllum*, together with the genera *Eriophyllum* Lag. and *Phialis* Spreng., in the genus *Bahia*. In a later paper Nuttall (1841), contrary to the present Code of Botanical Nomenclature, adopted the name *Bahia* for the North American elements of the genus and proposed the name *Stylesia* for the South American ones. This nomenclatural arrangement persisted until 1874.

Gray (1874) interpreted the genus *Schkuhria* Roth. to embrace three sections, two of which included only annuals. He transferred some of the annual species of *Bahia* ("*Eriophyllum* section") to *Actinolepis* DC. and the remainder to one of the annual sections of *Schkuhria* while retaining the perennial species (including those of the "*Eriophyllum* section") in the genus *Bahia*. Subsequently, Gray (1884) undertook a critical appraisal of the generic distinctions between *Bahia*, *Eriophyllum*, *Schkuhria* and related genera. This was the first attempt to give some order to the total complex and to indicate the natural relationships among the included species. *Bahia*, which he differentiated from both *Eriophyllum* and *Schkuhria* by a combination of morphological characters, was newly interpreted to comprise three sections: (1) five suffruticose or perennial taxa, (2) two herbaceous species with perennial caudices, and (3) nine annual taxa. A yet more critical treatment of *Bahia* by Gray (1886) left unchanged his division of the genus into three sections. He

recognized 11 species and one variety in this final expression of his concept of the genus.

A number of new species were described in the interim between Gray and Rydberg. In Rydberg's (1914) treatment of *Bahia* however, only 11 species (including 2 newly described species) and no varieties were included because of his proposed generic segregates (e.g., *Achyropappus*, *Amauriopsis*, *Picradeniopsis*).

The present treatment holds to the essential unity of the genus as expressed by Gray while recognizing the validity of two of Rydberg's several generic segregates.

CHROMOSOMAL STUDIES

Chromosome counts of $n = 8, 11, 12$ and 24 have been reported for the genus *Bahia* (Turner, 1959; Turner and Johnston, 1961; Turner, Beaman and Rock, 1961). As a result of the present study, an even more interesting array has become evident: $n = 8, 11, 12, 18, 22,$ and 24 , plus a single count of $n = 10$ in a species (*B. schaffneri*) previously known to have only the haploid number of 8.³ A discussion of the taxonomic significance and phylogenetic interpretation of the chromosomal information is deferred until later in this chapter.

Methods. Collections of buds for chromosomal studies were made in the field during the summers of 1959 and 1960.⁴ Chromosome counts were likewise made from collections which were grown in the garden for chromatographic and fertility studies. In all instances, the buds were fixed in a modified Carnoy's solution (4 parts chloroform: 3 parts absolute alcohol: 1 part glacial acetic acid) and placed under refrigeration as soon as possible. Buds remained in this solution for a period varying from several hours to several weeks. Entire florets were subsequently squashed in an aceto-orcein lactic acid stain (0.5% orcein in a solution of 1 part glacial acetic acid: 1 part lactic acid: 1 part water).

³Since the completion of this study by the writer, a count of $n = 36$ for *B. absinthifolia* var. *dealbata* has been made by A. M. Powell (Turner 4749).

⁴Voucher specimens are deposited in the University of Texas Herbarium.

Camera lucida drawings were made at magnifications of ca. $\times 1,500$.

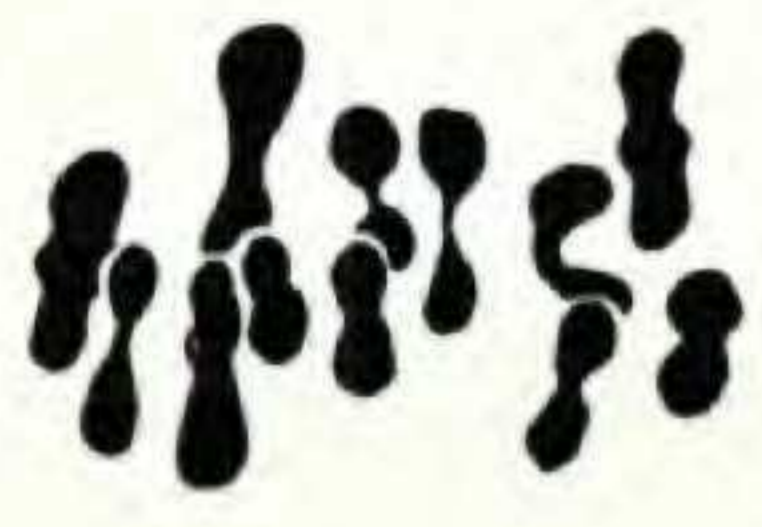
Results. *B. absinthifolia* var. *absinthifolia* has been reported to have a chromosome number of $n = 12$ (Turner and Johnston, 1961; Turner, Beaman and Rock, 1961). Information derived from this study indicates that a number of $n = 24$ is more common, the diploid populations being found only in the Mexican states of Nuevo León and San Luis Potosí. No morphological distinctions between the diploids and tetraploids were apparent in the field or in subsequent study of the vouchers. Similarly, a previous account (Turner and Johnston, 1961), has reported $n = 24$ for *B. absinthifolia* var. *dealbata*. Whereas the tetraploid number is the more prevalent, diploid populations were found in this variety as well. A single count of $n = 36$ is reported from Arizona (Turner 4749). I have made an approximate count of $n = 26$ from a single Texas population (*E. & T. 14*)⁵ and Turner (unpublished) has found a similar count from a Mexican population (Rock 483). Additional data are needed in order to discuss adequately the geographic distribution of both varieties of *B. absinthifolia* with regard to their chromosomal numbers. Karyotypic studies and further genetic tests should prove to be most informative.

Confirmation was made of $n = 12$ for *B. pedata* and $n = 8$ for *B. schaffneri*, the original counts having been reported by Turner and Johnston (1961). The additional chromosome

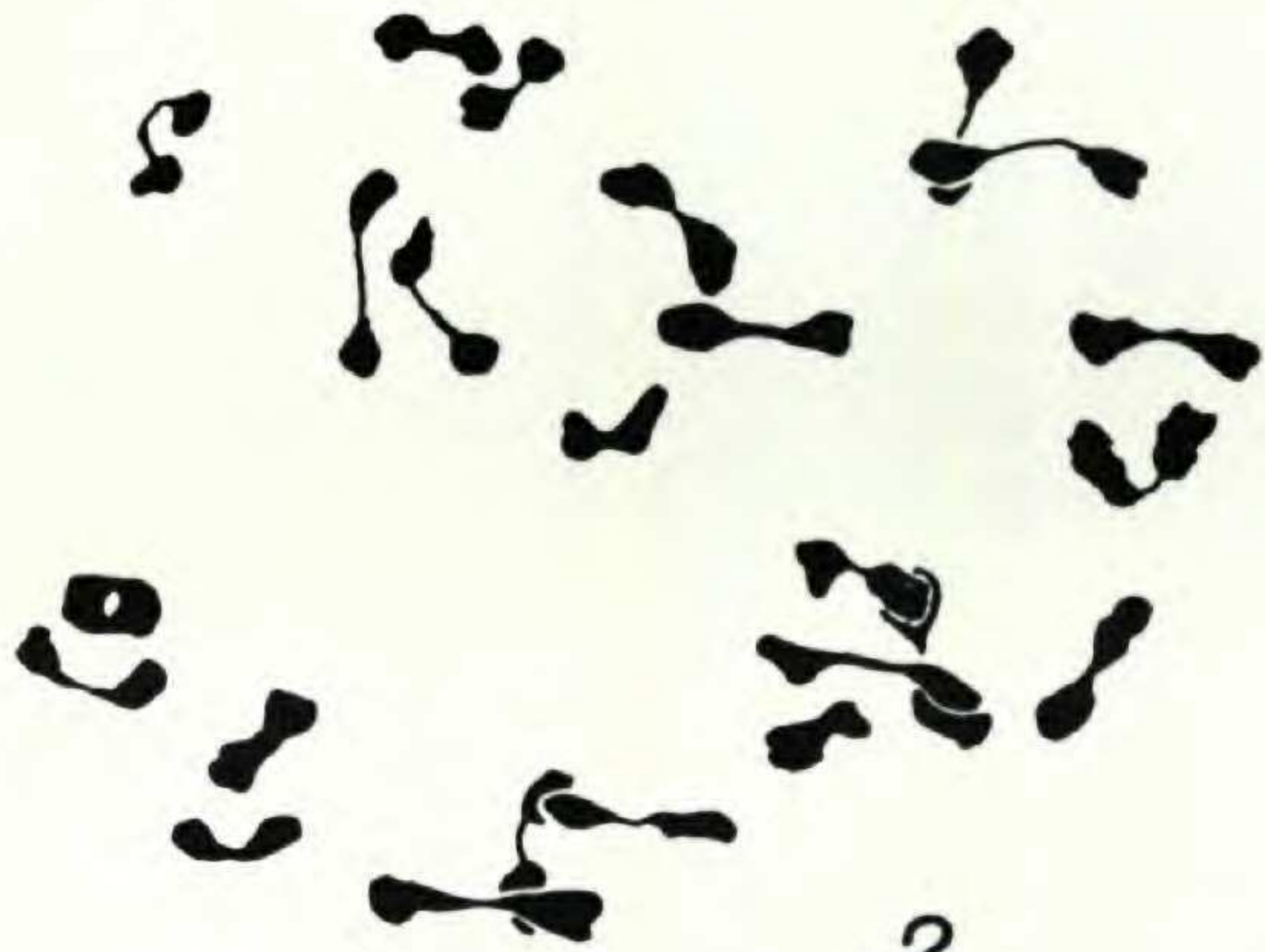
Fig. 1-8. Camera lucida drawings of meiotic chromosomes of taxa of *Bahia*. All ca. $\times 900$. Fig. 1. *B. absinthifolia* var. *absinthifolia*, $n = 12$, metaphase I (Johnston 4214B). Fig. 2. *B. a.* var. *absinthifolia*, $n = 24$, diakinesis (*E. & G. 114*)⁶. Fig. 3. *B. a.* var. *dealbata*, $n = 12$, diakinesis (*E. & T. 24*). Fig. 4. *B. a.* var. *dealbata*, $n = 24$, metaphase II (*E. & T. 13*). Fig. 5. *B. a.* var. *dealbata*, $n = 36$, metaphase I (Turner 4749). Fig. 6. *B. bigelovii*, $n = 11$, diakinesis, (*E. & T. 19*). Fig. 7. *B. pringlei*, $n = 22$, metaphase I, (*E. & G. 83*). Fig. 8. *B. xylopoda*, $n = 11$, metaphase II, (Johnston 4051A).

⁵The initials *E. & T.* are used throughout this study to designate collections by *W. L. Ellison* and *B. L. Turner*.

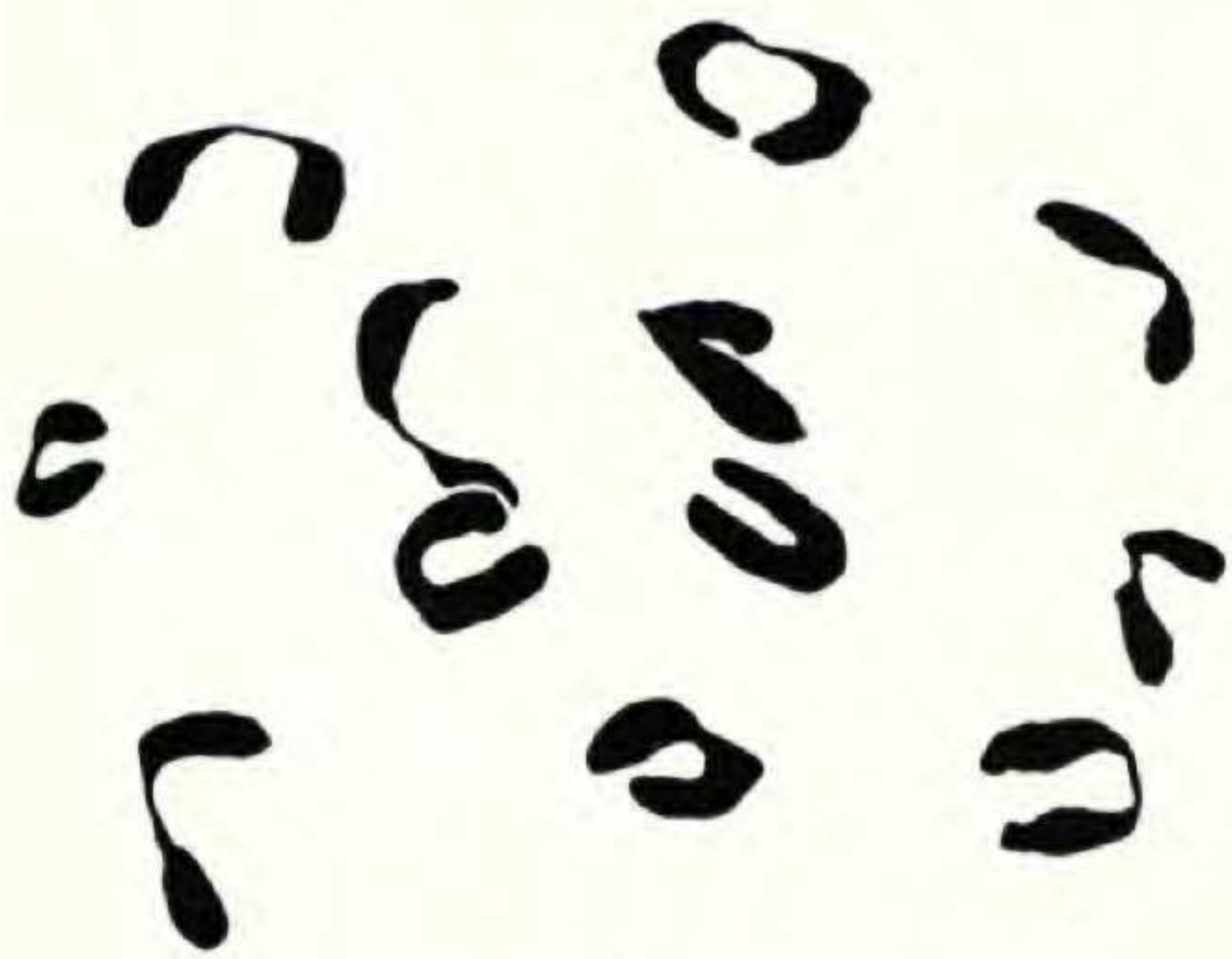
⁶The initials *E. & G.* are used to designate collections by *W. L. Ellison* and *A. Garcia*, *E. & T.* to designate collections by *W. L. Ellison* and *B. L. Turner*.



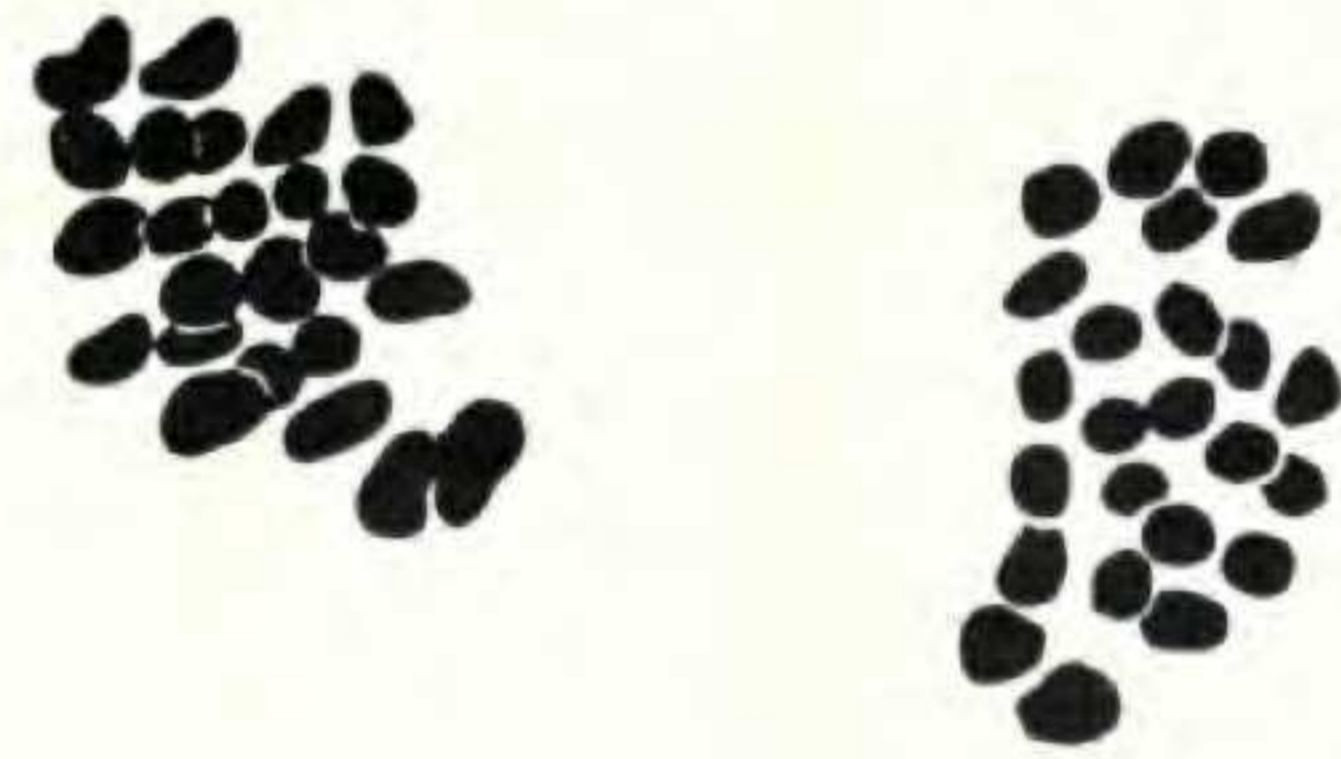
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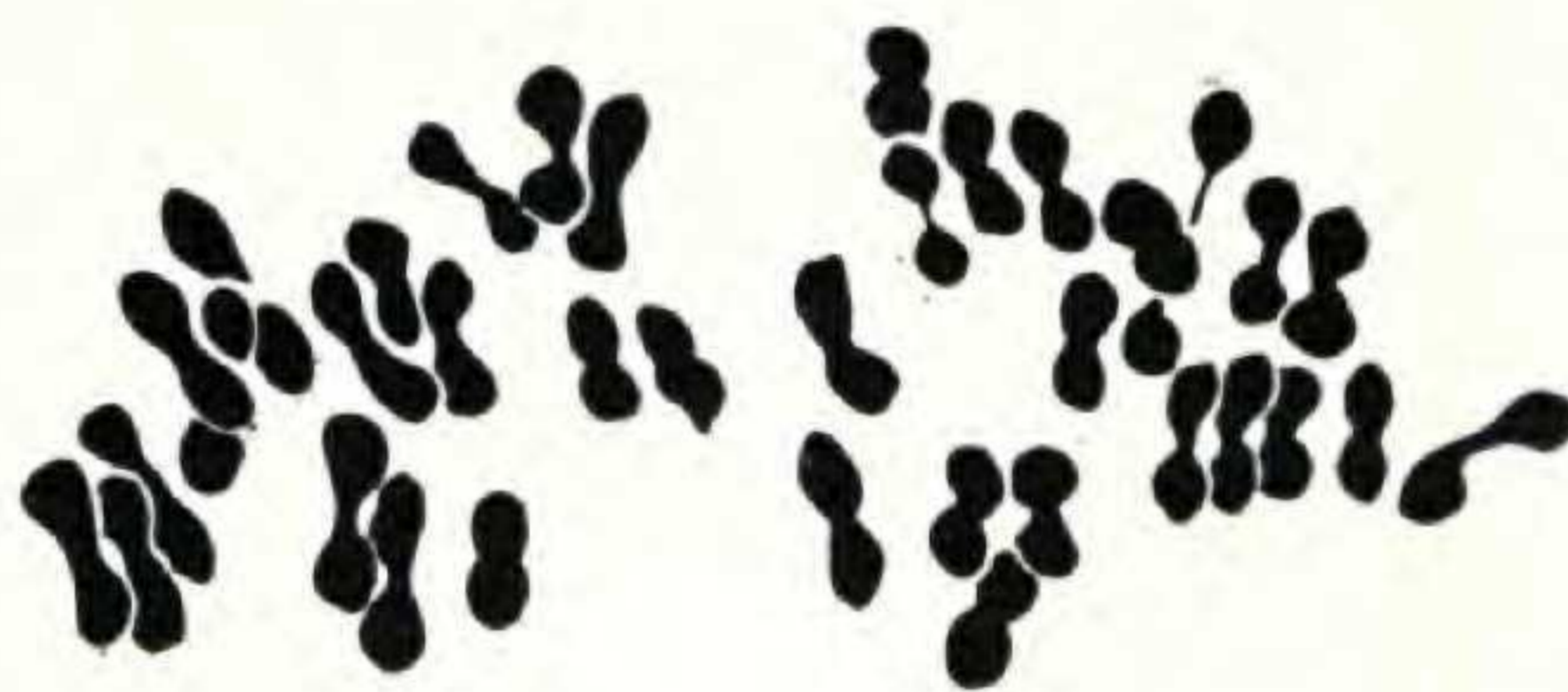
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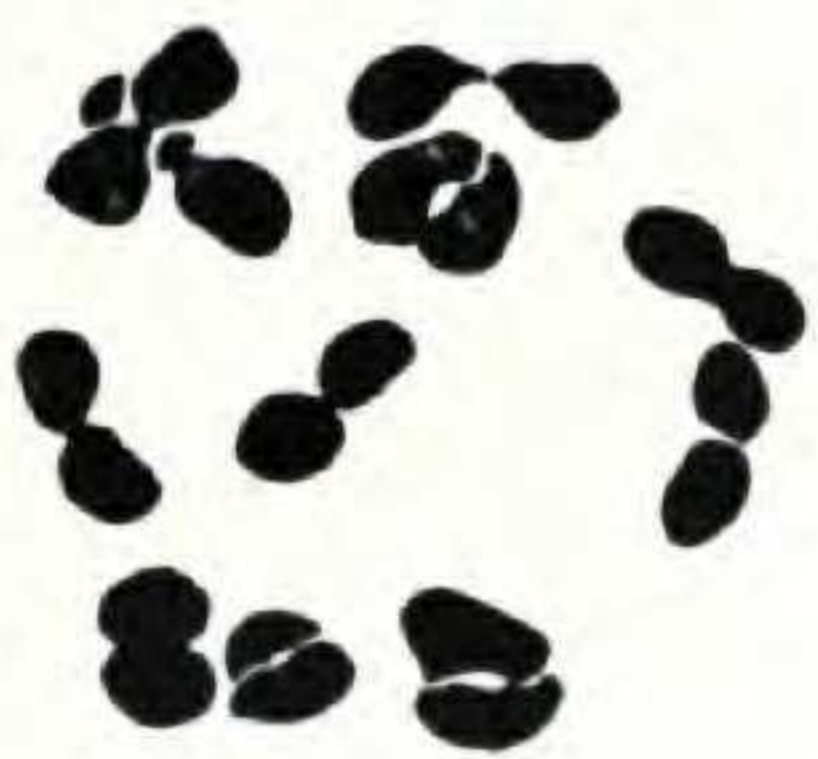
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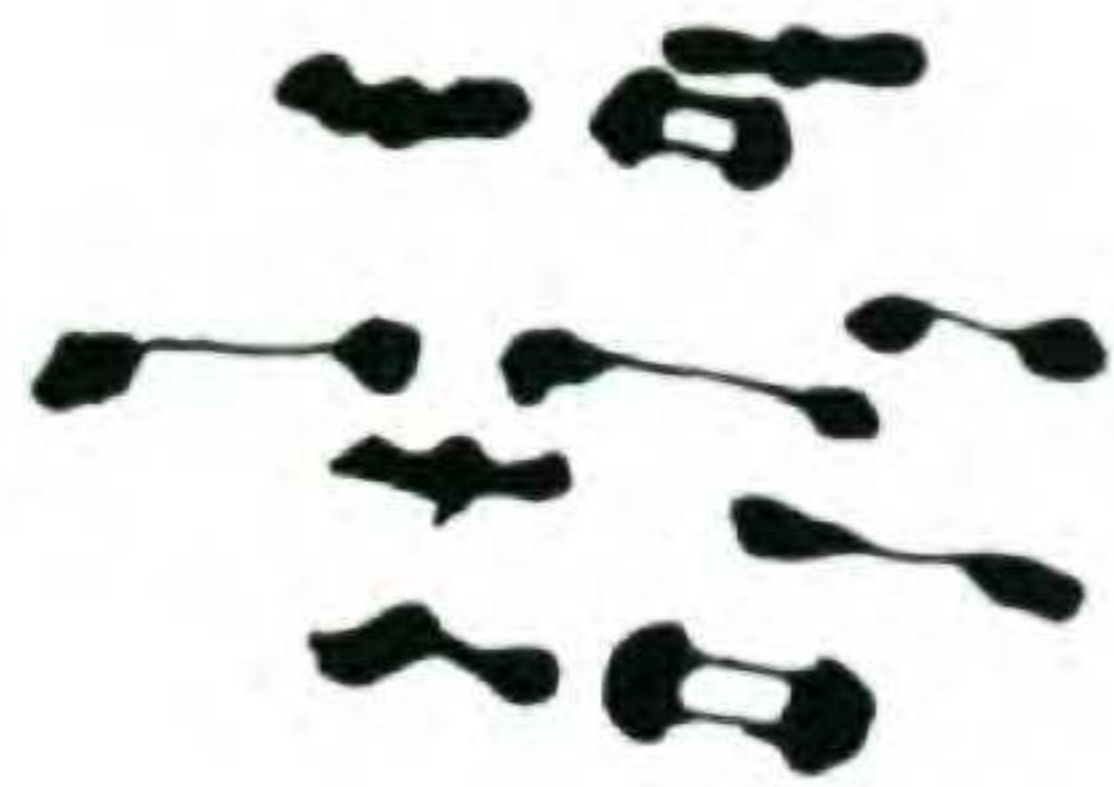


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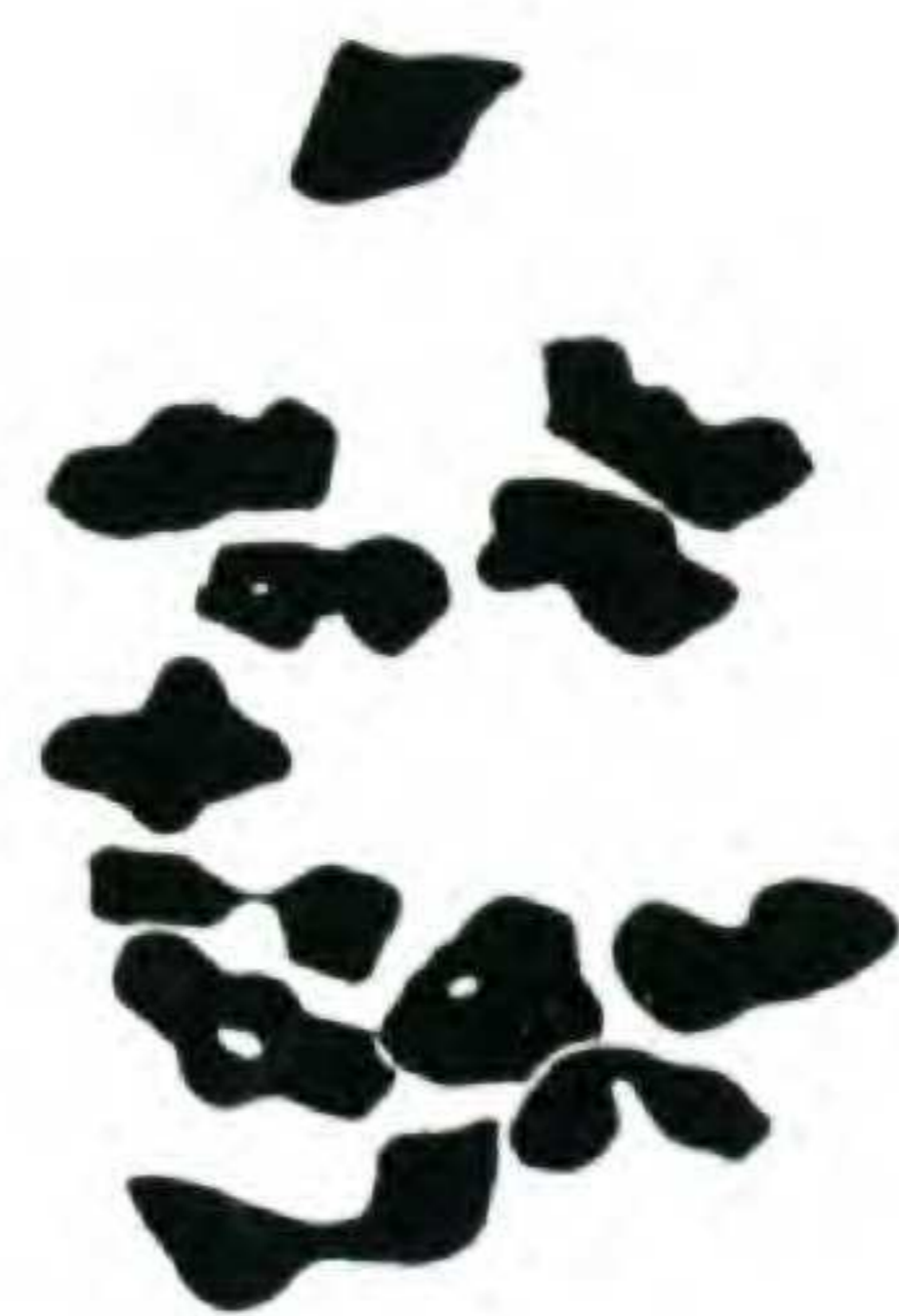
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16

number of $n = 10$ for *B. schaffneri* presents an interesting problem for future study. *B. xylopoda* was confirmed to have a chromosome number of $n = 11$, as originally reported by Turner, Beaman and Rock (1961). Turner and Johnston (1961) indicate a haploid number of $n = 11$ for *B. pringlei*; a study of the voucher sheets indicates that these are to be attributed to *B. xylopoda*.

In all the collections from which meiotic counts were made, pairing was regular with the exception of a ring of 4 in most plants examined from a single population of *B. pringlei* (E. & G. 78). Chromosome fragmentation was occasionally encountered in *B. absinthifolia* var. *dealbata*.

In addition to determinations of chromosome numbers for species of *Bahia*, counts were made of taxa in the related genera *Schkuhria* and *Achyropappus*. The South American *S. multiflora* has been reported to have a number of $n = 11$ (count by Schnack and Covas, 1947). The present count of $n = 11$ for the North American element constitutes additional evidence to substantiate Heiser's (1945) treatment of this bicentric species.

Eight different chromosome numbers are currently known for *Bahia*, and thus the genus lends itself quite well to phylogenetic speculations based upon such information. One may hypothesize a base number of $x = 8$ for the genus. Under this supposition *B. schaffneri* would be diploid ($2x = 16$) and *B. autumnalis*, *B. glandulosa* and *B. pedata* triploids ($3x = 24$). *B. absinthifolia* var. *absinthifolia* and var. *dealbata* would be either triploid, hexaploid ($6x = 48$) or enneaploid ($9x = 72$). *B. dissecta* ($n = 18$) could be of hybrid

Fig. 9-17. Camera lucida drawings of meiotic chromosomes of species of *Bahia*, *Schkuhria* and *Achyropappus*. All ca. $\times 900$. Fig. 9. *B. schaffneri*, $n = 8$, diakinesis (E. & G. 71). Fig. 10. *B. schaffneri*, $n = 10$, anaphase I (E. & G. 109). Fig. 11. *B. autumnalis*, $n = 12$, diakinesis (Johnston 4241). Fig. 12. *B. dissecta*, $n = 18$, metaphase II (E. & T. 22). Fig. 13. *B. glandulosa*, $n = 12$, diakinesis (King 3737). Fig. 14. *B. pedata*, $n = 12$, diakinesis (E. & T. 29). Fig. 15. *S. multiflora*, $n = 11$, metaphase I (Ellison 171). Fig. 16. *S. schkuhrioides*, $n = 8$, diakinesis (E. & G. 107). Fig. 17. *A. anthemoides*, $n = 10$, anaphase I (E. & G. 93).

origin, the hypothetical parents being triploid and hexaploid. *B. bigelovii* and *B. xylopoda* would be aneuploids derived from hypothetical triploid ancestors ($3x-2 = 22$ or $n = 11$); *B. pringlei* ($n = 22$) could then be assumed to have arisen as a tetraploid from this aneuploid line. No explanation is offered to account for the chromosome number of $n = 10$ found in the single population of *B. schaffneri*; however, it should be noted that a similar but more striking example may be found in the genus *Hymenoxys* where *H. odorata* has morphologically similar populations with counts of $n = 11$ and $n = 15$ (Turner, Beaman and Rock, 1961).

According to the views of Turner, Ellison and King (1961), it is perhaps more probable that the ancestral number is $x = 4$. Thus, *B. schaffneri* would be a tetraploid ($4x = 16$), *B. autumnalis*, *B. glandulosa* and *B. pedata* hexaploids ($6x = 24$), and *B. absinthifolia* either hexaploid, 12-ploid ($12x = 48$), or 18-ploid ($18x = 72$). It seems probable that the 18-ploid *B. absinthifolia* was derived from hexaploid and 12-ploid parents of this species. *B. dissecta* could have been variously derived as a hybrid from hypothetical hexaploid and 12-ploid parents or as an allopolyploid from triploid and hexaploid parents. *B. bigelovii* and *B. xylopoda*, as noted in the previous paragraph, may be considered to have been derived by aneuploid loss with *B. pringlei* a result of doubling of the aneuploid number. This phylogenetic scheme of relationships is pictured diagrammatically in Fig. 18 for the 10 taxa for which counts are known.

Rather than assuming a base number of 4 or 8, one could select the number 6. Based on $x = 6$, he would have tetraploids ($4x = 24$), a single hexaploid ($6x = 36$), octoploids ($8x = 48$), and a single 12-ploid ($12x = 72$), in addition to the two numbers derived from aneuploid loss. The $2n = 16$ chromosome number could presumably be derived by aneuploid gain or loss, but no aneuploid series exists to lend credence to this hypothesis. Against the hypothetical base of 6, too, is the fact that no diploids ($2x = 12$) are currently known for *Bahia* or any of the related genera in the subtribe Bahianae. The ploidy levels do lend support to the hypotheti-

cal base of 6, however, there being no necessity for assuming the origin of spontaneously occurring, fertile triploids. Both the triploid taxa and the single hybrid species as proposed for the base number 8 present theoretical problems of fertility. This problem is likewise encountered, but only for the single species *B. dissecta*, when the base number $x = 4$ is assumed.

TABLE I. Chromosome Numbers in the Genera *Bahia*, *Schkuhria* and *Achyropappus*.

B. absinthifolia var. *absinthifolia*. $n = 12$: MEXICO, NUEVO LEON, Johnston 4214B, *E. & G.* 50, 56, SAN LUIS POTOSÍ, *E. & G.* 57, 58. $n = 24$: AGUASCALIENTES, *E. & G.* 108, DURANGO, *E. & G.* 116, 127, NUEVO LEON, *E. & G.* 55, SAN LUIS POTOSÍ, *E. & G.* 64, 70 ZACATECAS, *E. & G.* 112, 114.

B. absinthifolia var. *absinthifolia* > *dealbata*. $n = 24$: MEXICO, CHIHUAHUA, *E. & G.* 153.

B. absinthifolia var. *dealbata*. $n = 12$: TEXAS, *E. & T.* 28. $n = 12 + 2B$: TEXAS, *E. & T.* 27. $n = 24$: TEXAS, *E. & G.* 34, *E. & T.* 13, 15; MEXICO, CHIHUAHUA, *E. & G.* 138, COAHUILA, *E. & G.* 48. $n = 36$: ARIZONA, Turner 4749 (count by A. M. Powell).

B. bigelovii. $n = 11$: TEXAS, *E. & G.* 169, *E. & T.* 19.

B. dissecta. $n = 18$: TEXAS, *E. & T.* 22.

B. glandulosa. $n = 12$: MEXICO, DURANGO, *E. & G.* 118, 125, A. M. Powell & J. Edmondson 939 (count by A. M. Powell).

B. pedata. $n = 12$: TEXAS, *E. & G.* 168, *E. & T.* 16, 29; MEXICO, CHIHUAHUA, *E. & G.* 139.

B. pringlei. $n = 22$: MEXICO, HIDALGO, *E. & G.* 78, 83, 86, 90.

B. schaffneri. $n = 8$: MEXICO, GUANAJUATO, *E. & G.* 71, SAN LUIS POTOSÍ, *E. & G.* 65, 68, A. M. Powell & J. Edmondson 548 (count by A. M. Powell). $n = 10$: MEXICO, AGUASCALIENTES, *E. & G.* 109.

B. xylopoda. $n = 11$: MEXICO, HIDALGO, *E. & G.* 89, A. M. Powell & J. Edmondson 605 (count by A. M. Powell).

Schkuhria multiflora. $n = 11$: TEXAS, Ellison 171.

S. schkuhrioides. $n = 8$: MEXICO, GUANAJUATO, *E. & G.* 105, 107.

Achyropappus anthemoides. $n = 10$: MEXICO, MEXICO, *E. & G.* 93, 96, A. M. Powell & J. Edmondson 802 (count by A. M. Powell).

TESTS OF FERTILITY

Methods. Seeds collected during 1959 were germinated during January of 1960 on moist filter paper in petri dishes and were then transferred to greenhouse pots. Germination percentage was increased markedly through the use of kinetin (2-furfuryl amino purine) and gibberellin. Seeds were soaked for ten minutes in a solution of 3γ kinetin + 100γ

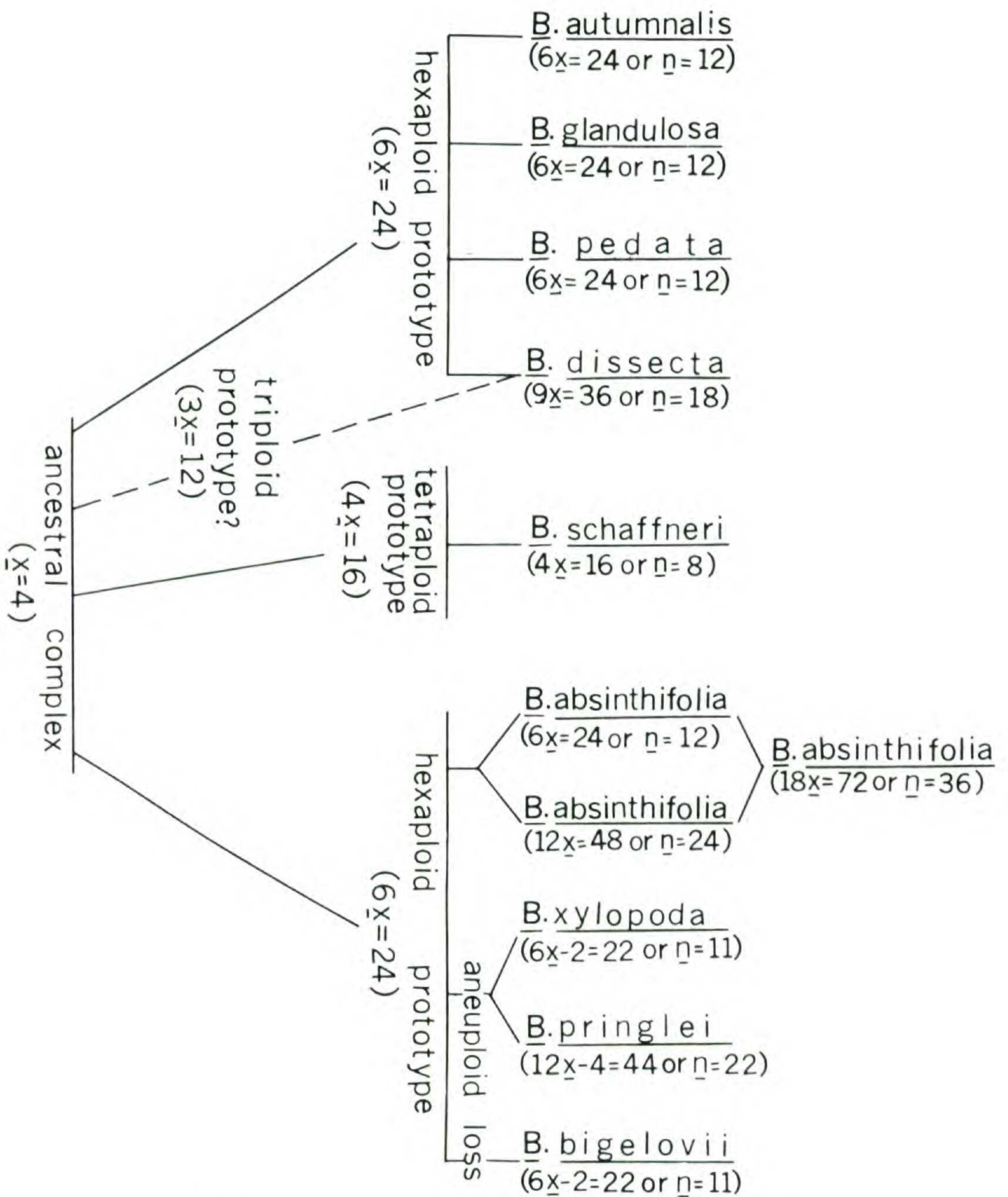


Fig. 18. Diagrammatic representation of a hypothetical phylogeny of *Bahia* based upon known chromosome numbers (additional explanation in text).

gibberellin per ml. water (Skinner, 1958). Following this treatment, the seeds were either placed directly in the petri dishes for germination, or dried and stored.

During the spring, some of the seedlings were transplanted to an outside garden and others were retained in the greenhouse. The following tests were applied: (1) self-sterility, (2) intra-specific and intra-varietal crosses, (3) inter-specific and inter-varietal crosses. Tests for self-sterility were made by bagging two heads before anthesis. If seeds formed in these heads, self-fertility was assumed. The intra-specific crosses were made to determine the effectiveness of the method employed in the inter-specific crosses.

Both the intra-/and the inter-specific crosses were made in the following manner. Heads were bagged while in bud and were left in the bags except at the time of crossing. The heads of two individuals were gently rubbed against one another on three different occasions (normally at daily intervals) as maturation of the florets progressed centripetally. Embryo development in four seeds or more in a head was interpreted as indicating a successful cross in taxa which were consistently found to set no seeds in previously determined self-sterility tests. Because of the occasional seed formation in presumed self-sterile plants (rarely 1 or 2 in a head), the results of the crosses should be interpreted with caution.

Results. Self-fertility tests: *B. absinthifolia*, *B. schaffneri* and *B. pedata* were found to be self-sterile or nearly so. *B. bigelovii*, *B. autumnalis* and *B. dissecta* were more or less self-fertile. The degree of self-fertility in these latter three taxa is summarized in Table II. The numerator and denominator in each ratio represent, respectively, the summation of the seed-set and the number of florets in two heads. As may be noted, 3 individuals of *B. bigelovii* and 4 individuals each of *B. autumnalis* and *B. dissecta* were tested.

Only one intra-specific or intra-varietal cross was made per taxon. This being the case, it is obvious that the results will be in the form of a doublet since each of the two heads used in the cross was examined for seed-set. The results

obtained are shown in Table III. No explanation is offered for the low seed-sets (particularly that of *B. absinthifolia* var. *absinthifolia*), though methodology and environmental conditions may have been contributory. It should be noted that the intra-specific percentage seed-set in *B. autumnalis* (and in *B. bigelovii* to a lesser degree) is significantly higher than the maximum seed-set in the tests of self-sterility. This is not true of *B. dissecta*, the percentage seed-set actually being higher in the self-fertility tests.

TABLE II. Results of Self-fertility Tests in Three Species of *Bahia*.

Species	Collection Number of Seed Source	Ratio of Seed-Set/Total Number of Florets
<i>B. bigelovii</i>	<i>E. & T. 19</i>	0/120 (= 0%); 0/162 (= 0%); 16/144 (= 11%)
<i>B. autumnalis</i>	<i>Johnston 4616</i>	2/338 (= 0.6%); 14/348 (= 4%) 14/244 (= 10%); 50/252 (= 20%)
<i>B. dissecta</i>	<i>E. & T. 22</i>	122/194 (= 63%); 154/220 (= 70%); 154/216 (= 71%); 190/234 (= 81%)

The data on the inter-specific crosses is summarized in Fig. 19. Two crosses between any two given taxa were made in every case. A diploid self-sterile *B. absinthifolia* var. *dealbata* ($n = 12$, *E. & T. 28*) appears here for the first time as I had only a single individual with which to work. The percentages refer to the female parent, and were calculated as follows:

$$\frac{\text{number of seed-set}}{\text{total number of florets}} \times 100$$

When no number appears, zero seed-set (rarely 1 or 2 seeds) is to be assumed. In all instances, the arrows point to the female parent. Solid lines graphically indicate the percentage seed-set in presumably successful crosses. Dashed lines indicate either the complete failure of seed-set, or, in the cases of *B. bigelovii*, *B. autumnalis* and *B. dissecta*, a seed-set equal to or less than their respective maximum seed-

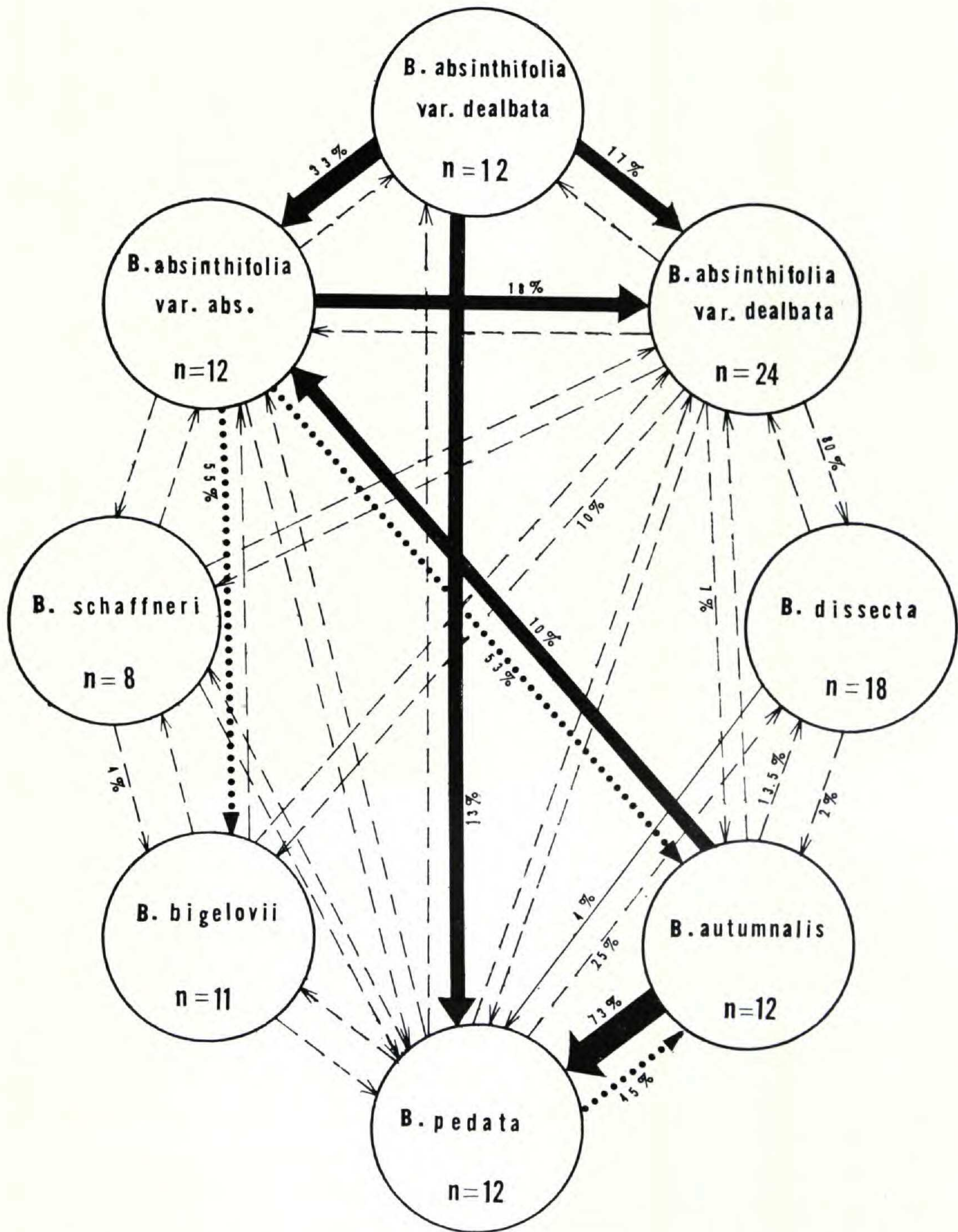


Figure 19. Inter-specific and inter-varietal tests of fertility in the genus *Bahia*. Solid lines denote significant seed-set in presumably successful crosses. Dashed lines indicate either complete failure of seed-set or a percentage which gave no positive evidence of crossability. Dotted lines denote dubious but possibly successful crosses (additional explanation in text).

TABLE III. Results of Intra-specific and Intra-variational Crosses in 7 Taxa of *Bahia*.

Taxon	Collection Number of Seed Source	Per Head Ratio of Seed- Set/Total Number of Florets
<i>B. absinthifolia</i> var. <i>absinthifolia</i> ($n = 12$)	Johnston 4214B	0/52 (= 0%); 5/54 (= 9%)
<i>B. absinthifolia</i> var. <i>dealbata</i> ($n = 24$)	E. & T. 15 E. & T. 34	32/85 (= 38%); 33/116 (= 28%)
<i>B. schaffneri</i>	Johnston 4029A	4/53 (= 8%); 11/45 (= 25%)
<i>B. bigelovii</i>	E. & T. 19	14/89 (= 16%); 24/44 (= 55%)
<i>B. pedata</i>	E. & T. 16	12/116 (= 10%); 35/92 (= 38%)
<i>B. autumnalis</i>	Johnston 4616	121/166 (= 73%); 113/135 (= 84%)
<i>B. dissecta</i>	E. & T. 22	35/114 (= 30%); 84/106 (= 79%)

set as determined in the tests of self-sterility. The dotted lines indicate doubtful, but possibly successful, crosses in which the seed-sets were greater than those determined for these taxa in the self-sterility tests. For example, in the cross between *B. absinthifolia* var. *absinthifolia* and *B. autumnalis*, a seed-set of 10% in the former taxon was interpreted as being successful since *B. absinthifolia* had been shown to be consistently self-sterile. On the other hand, a 53% seed-set in *B. autumnalis* was interpreted as being only possibly successful because self-fertility percentages as high as 20% (see Table II) had been found for this taxon.

The supposed hybrid seeds, saved for future study, failed to germinate. A lapse of approximately 15 months intervened between harvesting the seeds and planting them. Thus, final verification of the results of the crosses is lacking.

CHROMATOGRAPHIC STUDIES

Chromatographic patterns have been utilized in recent studies as possible indicators of species affinities. A quantitative expression of such data has been made with reference to the genus *Bahia* (Ellison, Alston and Turner, 1962). The reader is referred to this publication as well as to the doctoral thesis of the writer (Ellison, 1961) for detailed information on collection and chromatography of the plant

material, calculations and methods of presentation of the chromatographic data, and taxonomic interpretations of these data.

LEAF STUDY IN BAHIA ABSINTHIFOLIA

Leaf shape has been used by most workers as the most conspicuous of several characters for the separation of *B. absinthifolia* var. *absinthifolia* and *B. a.* var. *dealbata*. No population work having been conducted with respect to this character, it was thought early in this study that an investigation of leaf profiles would be helpful in determining not only the existing variability, but also the validity of the profiles in distinguishing between the two taxa.

Methods. A single leaf from the second internode below a mature inflorescence was taken from each of twenty plants in a population. The selection of plants was made in a "random" fashion so that the leaves might be as representative of the population as possible. Leaves were pressed, dried, and subsequently glued to cardboard. There was an attempt to place the leaves from each population in an order ranging from the simplest to the most complex. In some instances, due to the size of the leaves, the number used was necessarily reduced. In such instances near duplicates were deleted. In order that the profiles be clearly visible, the leaves themselves were covered with black india ink.

Population samples are arranged in a geographical fashion (Fig. 20-38), which, for the most part, conforms with the order of collection. Reference should be made to Fig. 39 for the locations of the populations considered.

Results. A number of facts are immediately discernible. One is the extreme variability of leaf width and dissection both within the species as well as within any given population. A second observation is that there are six populations (Figs. 20, 33, 35, 36, 37, 38) that show rather consistent broad-leaved segments. In addition, there is a correlative reduction in degree of segmentation. Reference to Fig. 39 indicates these collections are grouped in northern Mexico and western Texas. The remainder of the populations have more or less narrow-leaved segments and are generally more dissected. A basic similarity in all the populations is their

trifid nature, although simple entire leaves and other variations are common. An additional observation is that, within the above-mentioned six populations, there is, in most instances, at least one leaf pattern that is indistinguishable from one or more leaves in the narrow-leaved populations.

If one were to use leaf pattern alone for species distinction and employ selected single plants instead of populations, it is obvious that numerous taxa could be named. It is only by reference to populational patterns that meaningful biological decisions may be made. According to the present treatment, the six populations with the predominantly broad-leaved segments belong to *B. absinthifolia* var. *dealbata*; all others are *B. absinthifolia* var. *absinthifolia* with two notable exceptions, these being the samples represented by Figures 32 and 34. These samples were taken from what appeared to be intermediate populations of the two varietal taxa.

It is suggested that future single collections of these taxa include at least a few additional comparable leaves from various plants in the population so that the range of variation may be more apparent. To do so will aid immeasurably in rendering taxonomic decisions.

MORPHOLOGY AND TAXONOMIC CRITERIA

There are various salient features and combinations of characters that are useful in the circumscription of the species and varieties. Whereas full appreciation can come only from actual work in the field and study of herbarium material, a brief descriptive appraisal of the basic morphological features which mark *Bahia* is desirable.

HABIT. Species of series *Alternifoliae* are tall, erect, alternately leaved annuals or biennials. Those of series *Oppositifoliae* are shorter, erect to decumbent annuals or perennials with most or all of the leaves opposite.

ROOT. Perennial species have woody rootstocks which may or may not bear adventitious shoots. Annual and biennial species have taproots which normally bear single crowns at their apices. The roots of the perennial species are particularly diagnostic; special care should be taken in the collection of specimens in order that the rootstocks be included.

LEAVES. Leaf characters alone are adequate to differenti-

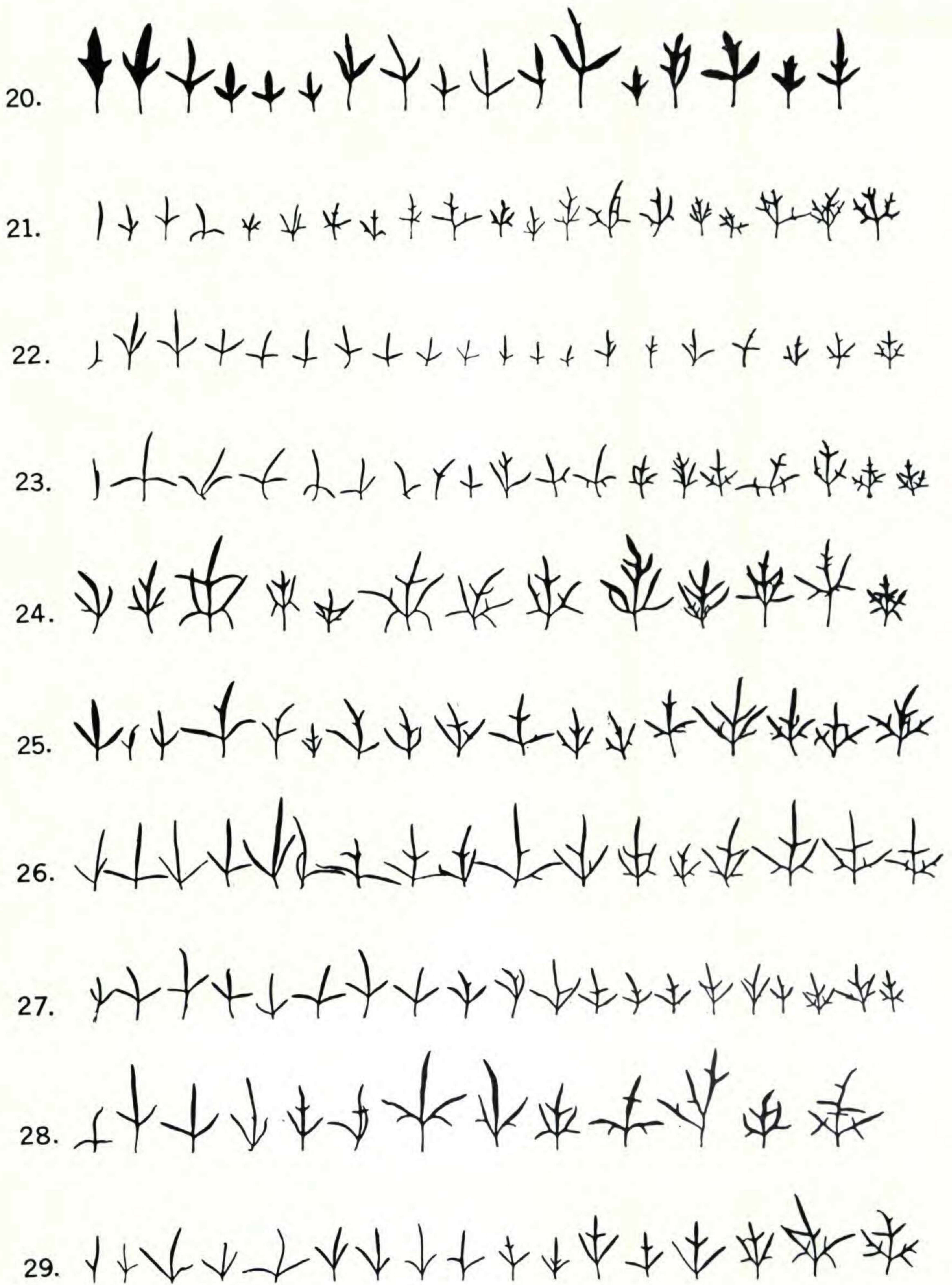


Fig. 20-29. Selected leaves from various populations of *B. absinthifolia*. (See Fig. 39 for the geographical locations of the collections.) All ca. $\times \frac{1}{2}$. *B. a.* var. *dealbata*: Fig. 20, *E. & G.* 48. *B. a.* var. *absinthifolia*: Fig. 21, *E. & G.* 50; Fig. 22, *E. & G.* 56; Fig. 23, *E. & G.* 58; Fig. 24, *E. & G.* 64; Fig. 25, *E. & G.* 70; Fig. 26, *E. & G.* 108; Fig. 27, *E. & G.* 112; Fig. 28, *E. & G.* 114; Fig. 29, *E. & G.* 116.

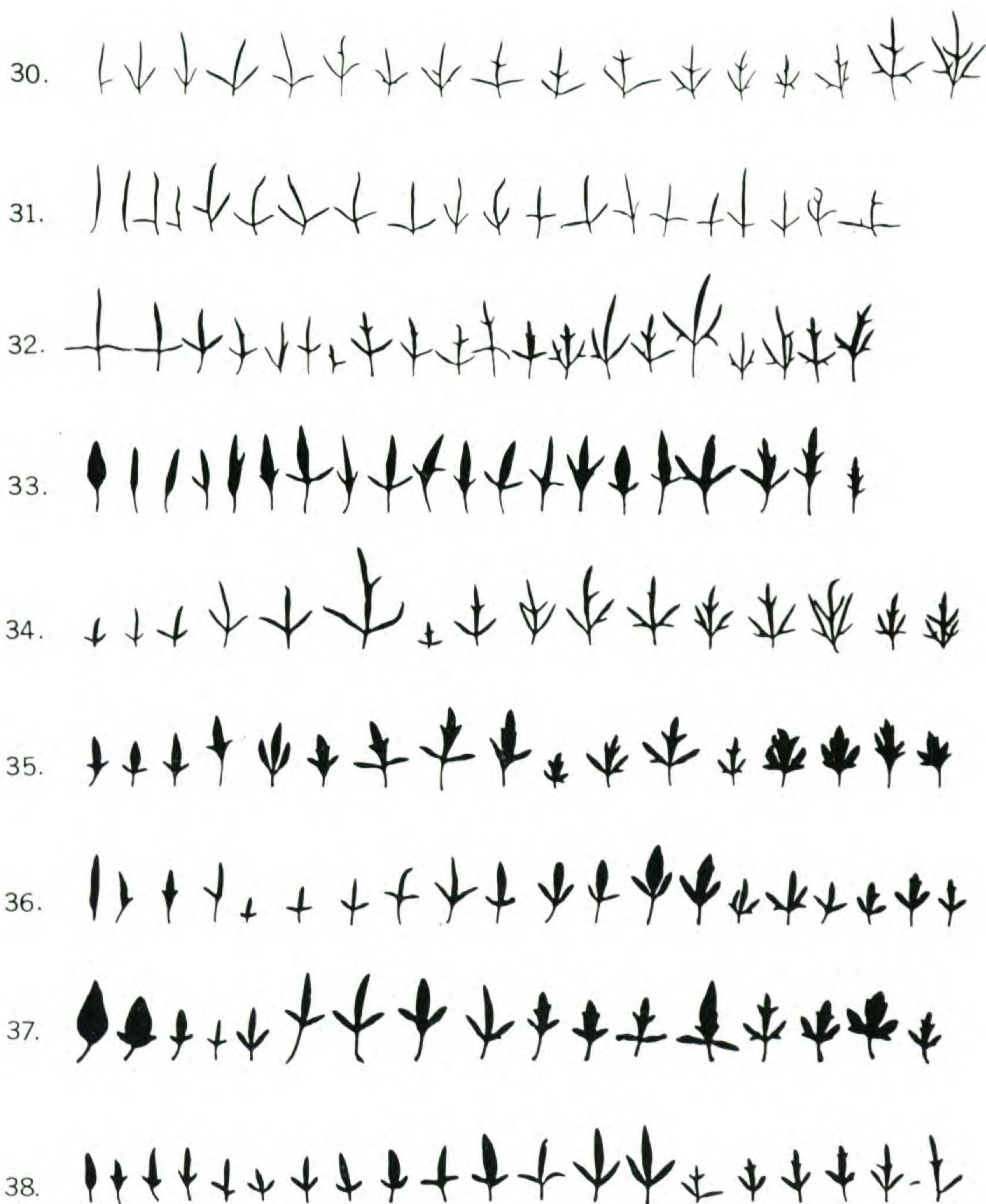


Fig. 30-38. Selected leaves from various populations of *B. absinthifolia*. (See Fig. 39 for the geographical locations of the collections.) All ca. $\times \frac{1}{2}$. *B. a.* var. *absinthifolia*: Fig. 30, *E. & G.* 127; Fig. 31, *E. & G.* 130. *B. a.* var. *absinthifolia* $>$ *dealbata*: Fig. 32, *E. & G.* 135; Fig. 34, *E. & G.* 153. *B. a.* var. *dealbata*: Fig. 33, *E. & G.* 138; Fig. 35, *E. & G.* 166; Fig. 36, *E. & T.* 27; Fig. 37, *E. & T.* 13; Fig. 38, *E. & T.* 42.

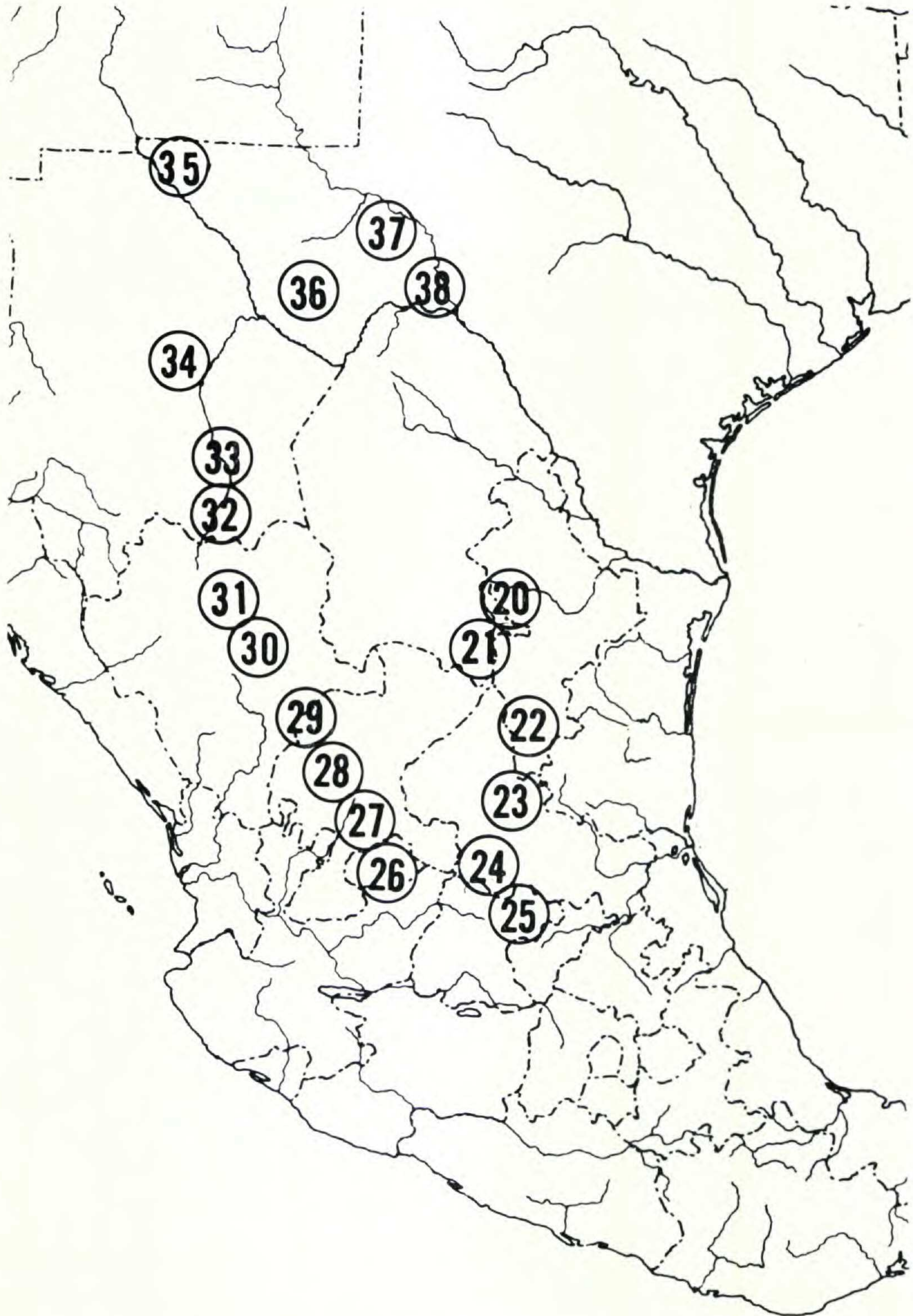


Fig. 39. Map showing locations of populations of *B. absinthifolia* var. *absinthifolia* and var. *dealbata* used in leaf study. (The numbers refer to Figs. 20-38).

ate between series *Alternifoliae* and series *Oppositifoliae* as well as to make certain specific determinations. The basic leaf pattern for the genus is trifid, although simple linear leaves occur on basal parts of some individuals in the species of the latter series.

INFLORESCENCE. All species have paniculate-cymose inflorescences with few to many heads.

HEADS. Only radiate heads are found in the genus. The size of the heads, number of disc and ray florets and, in some instances, the size and shape of the involucral bracts serve as distinguishing characters.

FLORETS. The disc corollas in all species are more or less broadly campanulate or funnelform and yellow or orange in color. The shape and size may be used as diagnostic features in certain species. With the exception of two taxa with white ray florets (one in each of the two series) all have yellow rays.

SUPERFICIAL PROCESSES. Pubescence and stipitate glands are of considerable taxonomic significance within the genus. One species in series *Oppositifoliae* can be identified on the basis of the degree of leaf pubescence alone, and stipitate glandulosity plus pubescence on vegetative parts is of considerable value in differentiating between some of the species in series *Alternifoliae*. Stipitate glands are present on the tube of the disc florets in all species and are of little value in the circumscription of the species.

ACHENES. All achenes in the genus are 4-sided and obpyramidal, although the peripheral ones are frequently somewhat incurved. Particular importance is attached to the number and shape of the pappus scales, and, in one species, to their predominant absence. Achenal pubescence and glandulosity are quite significant in the identification of certain taxa when used in conjunction with other characters.

STYLE BRANCHES. All style branches in the genus are flattened, having prominent marginal stigmatic lines and obtuse papillose appendages at their apices.

(To be concluded)